COMMUNICATION BY CUTICULAR PHEROMONES IN A LINYPHIID SPIDER

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ABSTRACT

The bowl and doily spider, *Frontinella pyramitela* (Araneae, Linyphiidae), receives information about its world primarily through its senses of touch (including vibrations) and taste. We report here that when a male touches the carcass of a conspecific mounted on the web of an adult female, the male receives information about the sex of the carcass. Moreover, the information is encoded in chemical form on the cuticles of both sexes of adult spiders. Tarsal contact with the carcass of a male elicits many abdomen flexions but few foreleg waves from an assay male. In contrast, tarsal contact with the carcass of a female elicits far fewer abdomen flexions but many foreleg waves. Both intersexual differences are lost when the carcass has been washed in solvent.

INTRODUCTION

A growing literature on communication by web-building spiders suggests that the vibratory (reviewed by Barth 1982) and chemical (reviewed by Tietjen and Rovner 1982) channels are of primary importance. Among the solitary web-builders, vibratory and/or pheromonal communication are usually associated with agonistic interactions (e.g., Christenson and Goist 1979; Riechert 1984), mate attraction and courtship (e.g., Krafft 1978; Olive 1982; Roland 1984), or parent/offspring relations (e.g., Norgaard 1956; Tretzel 1961; Krafft and Horel 1980), those being the only situations in which intraspecific communication typically occurs. The literature on communication in social spiders is more sparse, but there, too, the same two channels appear to be of primary importance (Kullmann and Zimmermann 1971; Buskirk 1975; Lubin in press).

The bowl and doily spider, *Frontinella pyramitela* (Walckenaer) (Araneae, Linyphiidae), is a solitary spider that also appears to utilize vibrations and pheromones as its primary communication signals. This spider's male-male agonistic interactions are characterized by nearly continuous vibratory signalling which may culminate in tactile displays (Austad 1983; Suter and Keiley 1984). Female-female agonistic interactions are also known in this species and they, too, are primarily vibratory (Hodge 1987). The seasonally frequent male-female agonistic interactions that occur during disputes over access to prey in this species are also mediated by vibratory signals (Suter 1985). It has heretofor been unclear whether the communication during any of these agonistic interactions might involve pheromones in addition to vibrations, and whether the direct contact between contestants was chemically informative.

The courtship of bowl and doily spiders involves pheromonal and vibratory signals as well as direct contact (Suter and Renkes 1982, 1984). As with the agonistic interactions, it has not been clear whether direct contact between the prospective mates was functional as communication and whether, if so, it was purely tactile or was chemotactile.

Work on other spiders, both non-social and social, has suggested that chemicals borne on the integument may act as pheromones (Krafft 1975, 1982; Lubin in press). In the work reported here, we sought to determine whether the outer surfaces on adult *F. pyramitela* bear chemicals that function as pheromones in either agonistic or courtship contexts.

MATERIALS AND METHODS

Bowl and doily spiders are common inhabitants of fields and forest edges throughout much of North America. They are easily captured as adults from their concave upward, bowl-shaped webs, and can be maintained in the laboratory for weeks and sometimes months. Techniques used to maintain the animals in captivity are described elsewhere (Suter and Keiley 1984; Suter 1985).

In the laboratory, healthy female *F. pyramitela* build new webs every day if they are removed from their old ones and if they are well fed. By such removals and frequent feeding, we accumulated a number of clean (no prey carcasses or other debris) webs which later served as the arenas on which behavioral assays were run.

The complete assay arena consisted of a female-produced web and, cemented to it, the carcass of either a male or a female bowl and doily spider. The carcass was prepared in one of two ways: a live spider was dropped into absolute methanol and then into hexane, each for 30 minutes, and then was air dried for at least 24 h, or a live spider was impaled through the cephalothorax with a fine pin and then placed in a desiccator to dry for 24 h. Dried carcasses were mounted on the underside of the bowl of a web, the normal location of either sex of the species, with droplets of Testor's paint applied to the spider's tarsi. Several hours after carcass mounting, the completed arena was used in behavioral tests. (Preliminary testing of the dried paint indicated that it neither attracted nor repelled nor otherwise affected the behavior of bowl and doily spiders.)

At the start of a behavioral assay, the assay spider, a male, was swung at the end of its dragline onto the upper strands of the web. In response to a web-borne pheromone (Suter and Renkes 1982), it would then proceed downward until it made contact with the silk of the bowl and then laterally until it could reach the lip. Once on the underside of the bowl, the assay spider would, through oriented search behavior (Suter 1984), quickly arrive at the center and make contact with the carcass mounted there. The timing of a 5-minute behavioral assay began upon contact with the carcass. The initial contact and all subsequent behaviors were videotaped from above while a voice record of the behaviors visible from the side of the web was made on one of the tape's audio channels.

We analyzed the videotapes with respect to two stereotyped male behaviors. One behavior, the abdomen flexion, is known to be characteristic of males both during courtship (Suter and Renkes 1982, 1984) and during agonistic interactions (Austad 1983; Suter and Keiley 1984). The other, the foreleg wave, is seen only during courtship and then usually late in courtship (Suter and Renkes 1984).

RESULTS

Initial contact of the assay male with a carcass usually involved the tarsi of the assay animal and the legs of the carcass. Subsequent contacts, especially during tests in which the assay male was foreleg waving, also involved contact with the body of the carcass, and occasionally the assay animal's pedipalps and mouthparts touched the carcass. Rarely, the assay male fed for a brief period on a carcass.

Untreated male carcasses and untreated female carcasses elicited significantly different numbers of abdomen flexions (Fig. 1a) as well as significantly different amounts of foreleg waving (Fig. 1b) from assay males. During 5 minutes of post-contact activity, the male assay spiders produced nearly four times as many abdomen flexions in response to unwashed male carcasses (median = 224) as in response to unwashed female carcasses (median = 65.5; Mann-Whitney U test, $P < 0.01$). During the same test period, assay males did 27 times as much foreleg waving in response to unwashed female carcasses (median = 27 s) as in response to unwashed male carcasses (median = 1 s; Mann-Whitney U test, $P < 0.01$).

Treating male and female carcasses with methanol and hexane washes rendered them much more similar to each other than were the untreated carcasses. With respect to abdomen flexions, there remained a significant difference between washed males and washed females, but the direction of the difference was reversed. The washed carcasses of males elicited fewer abdomen flexions from assay males than did the washed carcasses of females (male median = 100, female median = 37; Mann-Whitney U test, $P = 0.03$). With respect to foreleg waves, the solvent treatment eliminated the difference between the sexes of the carcasses. The washed carcasses of both males and females elicited very little foreleg waving (median for each = O s; Mann-Whitney U test, $P = 0.82$) from the assay males.

DISCUSSION

The data presented here demonstrate clearly that male bowl and doily spiders perceive differences, based on touch alone, between male and female conspecifics. There is no a priori reason to assume that the sex discrimination is based upon chemical rather than structural differences, except that other aspects of the spider's behavior are strongly influenced by pheromones (see references in the introduction). Tests of solvent-washed male and female carcasses reveal that it is chemical differences between their surfaces, not structural differences, that elicit distinct behaviors from assay males: the untreated carcasses of males release far more abdomen flexions in assay males than do untreated carcasses of females (Fig. 1a), while both sexes of carcasses, when washed, release similar numbers of abdomen flexions; similarly, untreated carcasses of females release far more foreleg waving than do untreated male carcasses (Fig. 1b), while neither sex of carcass elicits much foreleg waving when it has been washed.

The assay male's response to contact with a dead spider on the web is consistent with its responses to contact with living conspecifics under natural conditions. When a male first contacts the web of a female, that contact releases abdomen flexions, which the male continues to produce until he contacts the female (Suter and Renkes 1982). The sequence of behaviors that follows contact is very complex, but in all cases that sequence includes foreleg waves whose
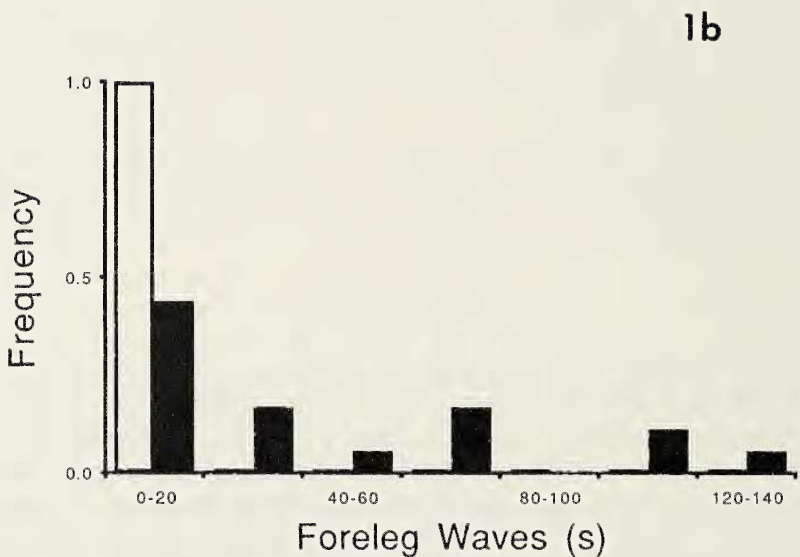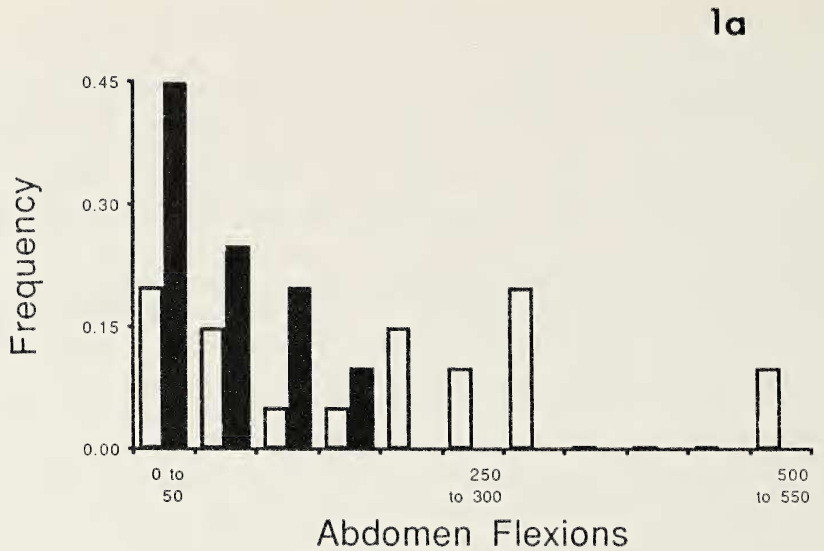
Fig. 1.—Behaviors performed by male assay spiders during the first 5 min following contact with the carcass of a conspecific. (a) Untreated male carcasses (open bars) elicited far more abdomen flexions than did female carcasses (filled bars), but (b) untreated female carcasses elicited much more foreleg waving (in seconds) than did male carcasses. With respect to both behaviors, when the carcasses had been washed in methanol and hexane, the sex-specific differences disappeared (see text).

frequency increases as courtship progresses (Suter and Renkes 1984). Thus it is not surprising that, if contact with a female's carcass is to elicit any sex-specific behavior, the behavior should be foreleg waving.

Parallel logic can be applied to the behavior of a male after contact with another male. The presence of a living male on a female's web ultimately leads, under natural conditions, to a stereotyped, agonistic interaction between the intruding male and the resident male (Suter and Keiley 1984). Such interactions,

though they may escalate to more intense displays and overt combat (Austad 1983; Suter and Keiley 1984), always include persistent abdomen flexion production. Again, it is no surprise that a male's contact with a dead male spider, if it is to elicit any sex-specific behavior, should elicit the production of more abdomen flexions.

Both courtship and male-male agonistic interactions in bowl and doily spiders are complex chains of behavioral events that involve vibratory communication as well as the contact chemical communication that we have now demonstrated. We deduce from this study and from our observation of attempted copulations by males on dead females and on female exuviae (Suter and Renkes 1984), that from the male's perspective, chemical confirmation that the resident spider is a female is both necessary and sufficient for courtship to reach completion. (It will be very difficult to similarly separate the roles of vibrations and chemicals either from the female's perspective in courtship or from either male's perspective in agonistic interactions.)

That the chemical confirmation is *sufficient* suggests that the role of the female in courtship is to delay copulation until she is fully ready, either physiologically or behaviorally, to mate. That the confirmation is *necessary* suggests that males are cautious, because prior to contact with the female they already have two sources of information about her identity. First, the webs of adult bowl and doily spiders are chemically marked such that an adult male knows whether a web it encounters was built by an adult male or by an adult female (Suter and Hirscheimer 1986), though the webs of juveniles are not easily distinguished, chemically, from those of adult females. Vibratory information, also available to the male spider shortly after he makes contact with an inhabited web, is similarly sex-specific (Suter and Renkes 1984; Suter and Keiley 1984) and thereby provides a second level of information about the probable identities of the inhabitants of a web. Now we have demonstrated that chemotactic information provides a third level.

That the third level is necessary for courtship to be completed implies that male *F. pyramitela* are cautious because of the detrimental consequences of close contact with a larger adult male or with a spider of another species. Evidence to be published elsewhere demonstrates that bowl and doily spiders also identify certain of their predators by detecting their cuticular chemicals (Suter et al. in preparation).

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